Wilson Bull., 106(1), 1994, pp. 91–105

MIGRATING SHOREBIRDS AND HABITAT DYNAMICS AT A PRAIRIE WETLAND COMPLEX

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Abstract.—We examined the responses of migrating shorebirds to habitat dynamics in a wetland complex on the Great Plains during 1989–1992. Availability of habitat was variable within and between seasons, but fluctuations in habitat were dampened when wetlands were considered as a complex rather than individually. Shorebirds exhibited an ability to colonize available habitat opportunistically, to occupy wet mud/shallow water habitats that became available during their residency period regardless of wetland history, and to use wet mud/shallow water habitat almost immediately upon its appearance. We found a significant relation between number of shorebirds and the area of wet med/shallow water habitat, regardless of dramatic changes in habitat. Management for continental stopover sites for shorebirds requires the maintenance of complexes of potential habitat to assure resource alternatives for birds as local conditions vacillate. *Received 11 Jan. 1993, accepted 20 July 1993.*

During migration, several species of Arctic-breeding shorebirds use freshwater wetlands in the North American interior as staging or stopover sites for replenishing fat reserves. Without food resources to "refuel", these birds would be unable to complete their journeys to breeding or wintering grounds. The protection of stopover resources for migrating shorebirds is critical to the survival of many of these species (Myers 1983). The first step in this protection effort, the identification of sites that traditionally support large populations during migration and the protection of these sites as a network (Myers et al. 1987), is being undertaken specifically by the Western Hemisphere Shorebird Reserve Network and, in general, by other wetland conservation programs (Bildstein et al. 1991).

Shorebirds migrating across continental wetland habitats encounter temporally and spatially dynamic wetlands (Fredrickson and Reid 1990, Szaro 1990, Skagen and Knopf 1993). The dynamic and unpredictable nature of interior wetlands and the rapid rate of loss and alteration of wetlands in these regions (Tiner 1984, Dahl 1990) combine to make the above "reserve" management approach problematic. Species that use disjunct patches of changing habitat in an irregular fashion, as seen especially during migration, may be the most difficult to protect (Takekawa and Beissinger 1989).

In this paper, we evaluate the predictability of stopover sites in the Great Plains and responses of migrating shorebirds to habitat dynamics. We hypothesized that when resource availability changes rapidly, tran-

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sitory populations respond to wetland dynamics opportunistically rather than exhibit strong annual site fidelity. More specifically, if migrating shorebirds use habitats opportunistically, we expect them to use available habitat regardless of the recent wetland history. Thus, although some wetlands provide no wet mud/shallow water habitat for shorebird foraging during all or parts of sequential migration periods, we expect shorebirds to find and use these wetlands when wet mud/shallow water habitat again becomes available during migration. Second, we hypothesized that if habitats are constantly fluctuating and birds are opportunistic, a positive correlation between birds and wet mud/shallow water habitat would occur. Alternatively, shorebirds that use sites traditionally would be tied to habitats that may be marginal in some years, and no relationship between numbers of birds and area of wet mud/shallow water habitat would be apparent.

STUDY AREA AND METHODS

Quivira National Wildlife Refuge, Stafford County, Kansas (38°10′N, 98°40′W), is a 8830-ha refuge of the U.S. Fish and Wildlife Service (Fig. 1). Forests and croplands are interspersed with 30 water units ranging in size from 1 to 600 ha and Rattlesnake Creek that flows intermittently. Vegetation in and surrounding the wetlands includes wetland plant species in the genera *Distichlis, Spartina, Typha, Carex*, and *Juncus*.

Shorebirds occurring in water units and in extensive mudflats and marshes throughout the refuge were surveyed from a vehicle and on foot 1–2 times weekly during late summer-fall migration (August through mid-October) 1989–1991 and spring migration (April to early June) in 1990–1992. Because the survey areas are relatively open and unvegetated, we were able to make complete counts of shorebirds (see also Colwell and Oring 1988, Hands et al. 1991). When feasible, we identified all individuals. When large numbers occurred or when birds were too distant to identify individually, we estimated total numbers of birds categorized by relative body size. We extrapolated to the larger group based on subsamples of birds.

We estimated dimensions of wetland units from maps and by pacing. During surveys, we estimated the percentage of each unit that comprised the following habitat types: dry mud, wet mud, mud-water film (1–2 cm of water interspersed with mud), shallow water (2–8 cm), and deep water (>8 cm) and noted presence of vegetation. We collected information on habitat availability at Quivira NWR on ten small (<5 ha) water units that were present all six seasons and on eight additional ephemeral wetlands during one or more seasons (Fig. 1). We quantified habitat availability only in the small discrete water units, not in the more extensive mudflats and marshes on the refuge (Fig. 1).

We operationally define the terms "suitable habitat" and "suitable wetland" to refer to wet mud-shallow water habitats with little or no vegetation, habitats that are generally

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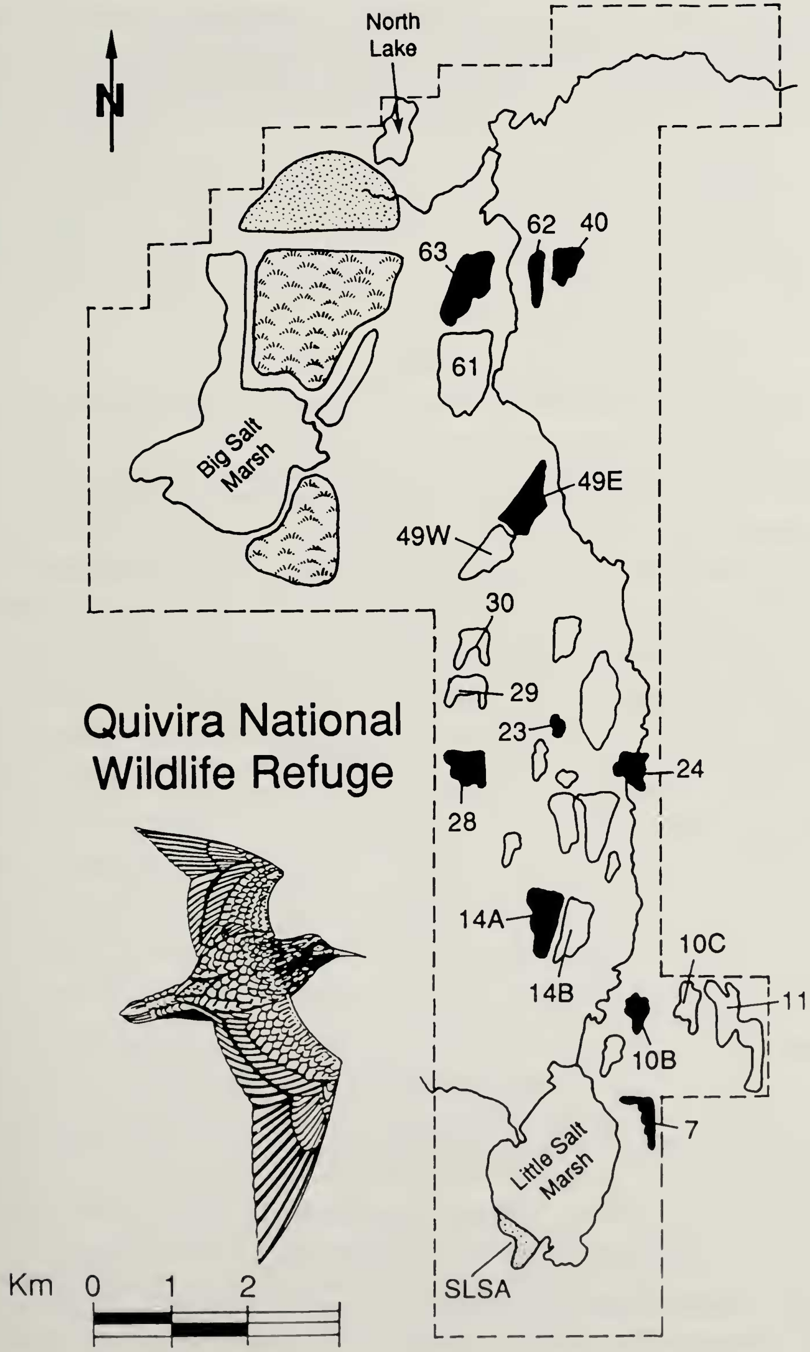
FIG. 1. Map of study site at Quivira National Wildlife Refuge, central Kansas. Eighteen individual water units are identified by number, and the ten units with extensive coverage are darkened.


N
North Lake
63
62
40
61
Big Salt Marsh
49E
49W
30
29
23
24
28
14A
14B
10C
11
10B
7
Little Salt Marsh
SLSA
Quivira National Wildlife Refuge
Km 0 1 2

attractive to most shorebird species (Colwell and Oring 1988). Below we use these terms interchangeably with "shorebird habitat" and "wet mud/shallow water."

We documented the sequential pattern of habitat availability in wetlands during six migration seasons, and noted shorebird use of wetlands that had no wet mud/shallow water habitat earlier in a season or in previous seasons. We also examined bird responses to the relative distribution of habitats in seasons when wet mud/shallow water habitat was available in water units. First, we selected five surveys in each season that corresponded with large increases in numbers of birds, suggesting the presence of new arrivals, and large overall counts on the refuge. Because many birds had recently arrived and because time intervals between these selected surveys averaged 12 days, we considered the surveys independent of each other. We formed three categories of shorebirds based on their primary patterns of habitat use (Table 1). All statistical analyses were performed using SYSTAT 5.0.

RESULTS

Quivira National Wildlife Refuge provided important stopover habitat for a total of 35 species during spring and late-summer/fall migrations (Table 1). During spring 1990, the season of heaviest shorebird use, peak counts totalled 15,633 birds. Peak numbers of individual species were generally higher in spring than in fall, and species composition varied between seasons. In both spring and fall, Long-billed Dowitchers (*Limnodromus scolopaceus*), Stilt Sandpipers (*Calidris himantopus*), Semipalmated Sandpipers (*C. pusilla*), and Wilson's Phalaropes (*Phalaropus tricolor*) were among the most common birds. White-rumped Sandpipers (*C. fuscicollis*) and Baird's Sandpipers (*C. bairdii*) were common only in spring, while Western Sandpipers (*C. mauri*) and Least Sandpipers (*C. minutilla*) were common only in fall. Shorebirds commonly associated with wet mud/shallow water habitat comprised more than 80% of peak numbers of birds (Table 1).

Habitat variability within and between seasons.—The condition of the wetlands varied considerably between the six migration seasons. During spring 1990, all units were full of water and had no wet mud/shallow water habitat suitable for shorebird foraging. In late summer–fall 1991, most small units were dry. Collectively, in a total of 74 unit-seasons (one water unit for one migration season), 36 had no wet mud-shallow water habitat. In 16 unit-seasons, wet mud/shallow water habitat was present initially but eventually disappeared, and in 18 unit-seasons, wet mud/shallow water habitat was absent initially but appeared later in the season. Only four unit-seasons had available habitat throughout a migration season.

The amount of wet mud/shallow water habitat in the water units often fluctuated during the 2–3 month migration season, as illustrated by 11 wetlands in fall 1990 (Fig 2). Because the amount of wet mud/shallow water habitat in individual wetlands was dependent on wetland topography and water levels, the presence of habitat across the various wetlands was not always synchronized (Fig. 2). At times, deeper wetlands had wet mud/shallow water habitat only during drying cycles when shallower wetlands completely dried. The patterns of water level fluctuations in individual wetlands were dramatically different between the six migration seasons (Fig 3).

However, fluctuations in the amount of wet mud/shallow water habitat were dampened at a larger geographical scale (Fig 4). As a result, there was high likelihood that wet mud/shallow water habitat was available in at least one wetland in the complex at a given point in time. Wet mud/shallow water habitat was generally available within the complex of 10 wetlands throughout four of the six migration seasons in this study (Fig. 5). When also considering the extensive mudflats and marshes on the refuge, suitable habitat occurred somewhere on the refuge in all six seasons.

Bird distribution relative to wetland history.—In general, shorebirds responded quickly to the first appearance of wet mud/shallow water habitat in a wetland in a given season (Table 2). In 15 of the 18 unit-seasons in which suitable habitat was absent initially but later appeared during that season, some shorebirds responded immediately (were present in the first survey after the appearance of wet mud/shallow water habitat). In only two cases, one survey elapsed before any shorebirds appeared, and in one case, shorebirds did not use the wetland at all, possibly because the habitat appeared late in the season when few birds remained in the area. Some species responded more consistently than others. Baird's Sandpipers, White-rumped Sandpipers, Lesser Yellowlegs (*Tringa flavipes*), and Long-billed Dowitchers appeared immediately in more than half the new suitable habitats in all seasons (Table 2), whereas Semipalmated Sandpipers and Least Sandpipers did not.

On average, only four days elapsed between the two surveys bracketing the appearance of habitat and birds. There was a broad range in numbers of individual birds that responded within the first few days of habitat availability (median = 28, range 3–1122). The species that occurred in the largest assemblages were Long-billed Dowitchers, Lesser Yellowlegs, Semipalmated Sandpipers, and Baird's Sandpipers.

Shorebirds also responded quickly to the first appearance of wet mud/shallow water habitat in a given wetland in several seasons (Table 2). During spring of 1992, three suitable wetlands had no wet mud/shallow water habitat during the preceding spring migration season, and four other suitable wetlands had no wet mud/shallow water habitat during two preceding spring seasons. In fall 1990, nine suitable wetlands had no wet mud/shallow water habitat during one preceding fall migration period. Even though no shorebirds had used these wetlands during spring (or fall)

TABLE 1

SHOREBIRDS AT QUIVIRA NATIONAL WILDLIFE REFUGE, KANSAS, DURING SIX MIGRATION SEASONS, 1989–1992, CATEGORIZED ACCORDING TO ASSOCIATION WITH THREE HABITAT TYPES

		Peak counts					
		Fall			Spring		
Alpha code	Common name (scientific name)	1989	1990	1991	1990	1991	1992
	Uplands, pond margins, dry mud						
SNPL	Snowy Plover (*Charadrius alexandrinus*)	83	85	74	118	104	112
PIPL	Piping Plover (*C. melodus*)	2	0	0	2	0	1
KILL	Killdeer (*C. vociferus*)	165	131	160	38	50	66
SPSA	Spotted Sandpiper (*Actitis macularia*)	15	8	18	23	20	31
UPSA	Upland Sandpiper (*Bartramia longicauda*)	3	2	0	2	1	1
BBSA	Buff-breasted Sandpiper (*Tryngites subruficollis*)	0	0	1	0	0	0
COSN	Common Snipe (*Gallinago gallinago*)	15	6	0	1	1	2
AMWO	American Woodcock (*Scolopax minor*)	0	0	0	2	0	0
	Wet mud–shallow water						
SEPL	Semipalmated Plover (*Charadrius semipalmatus*)	12	16	16	47	17	34
SESA	Semipalmated Sandpiper (*Calidris pusilla*)	664	600	561	1979	2470	3351
WESA	Western Sandpiper (*C. mauri*)	780	876	208	218	0	12
LESA	Least Sandpiper (*C. minutilla*)	1010	524	788	262	238	0
WRSA	White-rumped Sandpiper (*C. fuscicollis*)	0	0	0	5082	4867	1771
BASA	Baird's Sandpiper (*C. bairdii*)	258	229	189	1366	716	1284
BBPL	Black-bellied Plover (*Pluvialis squatarola*)	11	300	0	195	14	20
LEGP	Lesser Golden Plover (*P. dominica*)	7	0	1	10	0	2
GRYE	Greater Yellowlegs (*Tringa melanoleuca*)	122	122	100	155	221	184
LEYE	Lesser Yellowlegs (*T. flavipes*)	300	454	213	818	509	391
SOSA	Solitary Sandpiper (*T. solitaria*)	11	9	1	2	0	5
RUTU	Ruddy Turnstone (*Arenaria interpres*)	0	1	0	9	0	0

TABLE 1
CONTINUED

		Peak counts					
		Fall			Spring		
Alpha code	Common name (scientific name)	1989	1990	1991	1990	1991	1992
REKN	Red Knot (*Calidris canutus*)	9	0	0	0	0	0
SAND	Sanderling (*C. alba*)	17	39	5	22	0	0
PESA	Pectoral Sandpiper (*C. melanotos*)	68	37	49	105	44	20
DUNL	Dunlin (*C. alpina*)	0	0	1	25	5	0
STSA	Stilt Sandpiper (*C. himantopus*)	1152	713	68	1088	813	1175
SBDO	Short-billed Dowitcher (*Limnodromus griseus*)	0	0	0	5	0	0
LBDO	Long-billed Dowitcher (*L. scolopaceus*)	1165	1113	1975	1875	511	637
	Deeper and open water						
BNST	Black-necked Stilt (*Himantopus mexicanus*)	34	35	87	2	31	23
AMAV	American Avocet (*Recurvirostra americana*)	99	260	558	217	86	141
WILL	Willet (*Catoptrophorus semipalmatus*)	3	1	0	3	5	60
WHIM	Whimbrel (*Numenius phaeopus*)	0	0	0	6	0	16
HUGO	Hudsonian Godwit (*Limosa haemastica*)	0	0	0	3	10	51
MAGO	Marbled Godwit (*L. fedoa*)	0	3	0	2	13	9
WIPH	Wilson's Phalarope (*Phalaropus tricolor*)	216	621	356	1949	1895	2183
RNPH	Red-necked Phalarope (*P. lobatus*)	0	0	0	2	0	0
	All shorebirds	3246	3977	3601	6710	5477	5313
	Total of peak counts	6221	6185	5429	15,633	12,641	11,582
	Number of species	25	24	21	33	24	26

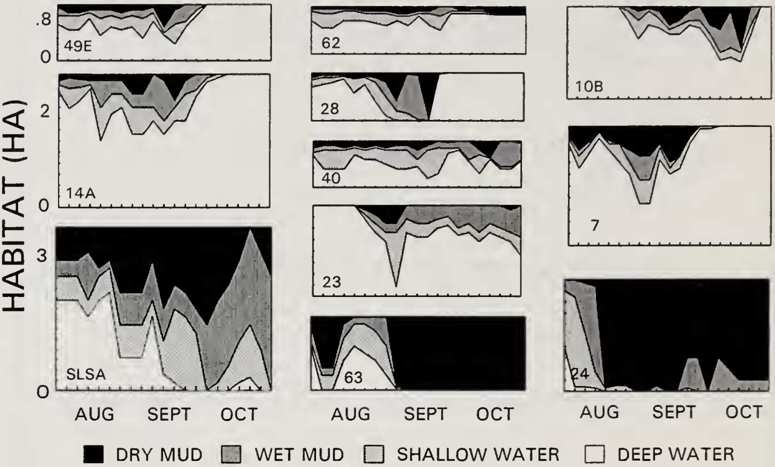


FIG. 2. Changes in availability of microhabitats (dry mud, wet mud, shallow water [<8 cm], and deep water [>8 cm]) in 11 wetlands through the late summer-fall migration season of 1990.

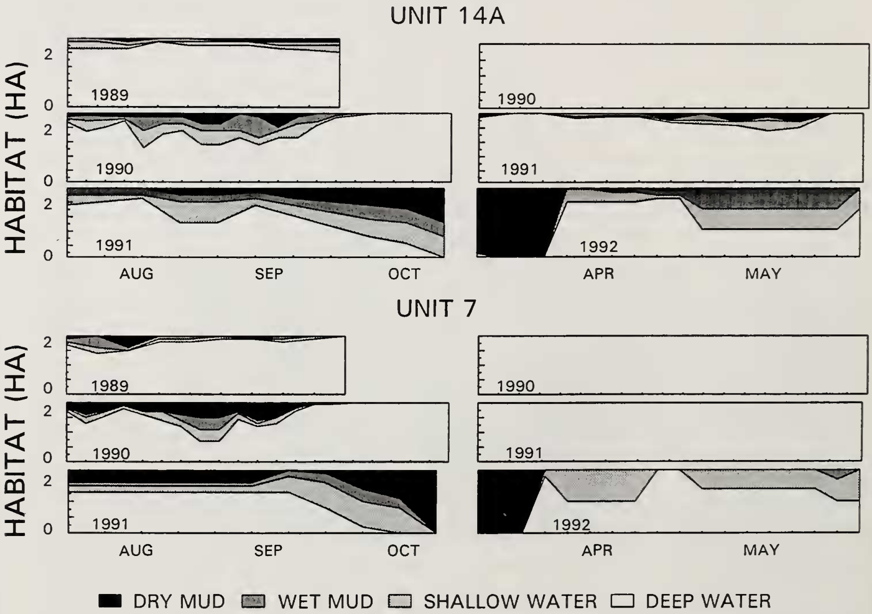


FIG. 3. Changes in availability of microhabitats (dry mud, wet mud, shallow water [<8 cm], and deep water [>8 cm]) in two wetlands throughout the six migration seasons of the study.

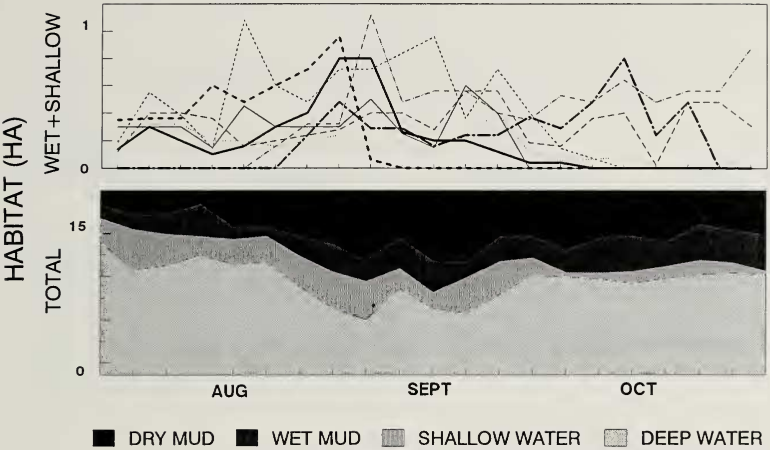


FIG. 4. (a) Amount of wet mud/shallow water (<8 cm) habitat in 11 wetlands through the 1990 fall season. (b) Total amount of wet mud/shallow water habitat across the 11 wetlands.

migration for 1–2 years, the first occurrence of wet mud/shallow water habitat coincided with the appearance of shorebirds (Table 2). As predicted, nearly all of the common species appeared in these wetlands once wet mud/shallow water habitat appeared, regardless of the recent wetland history.

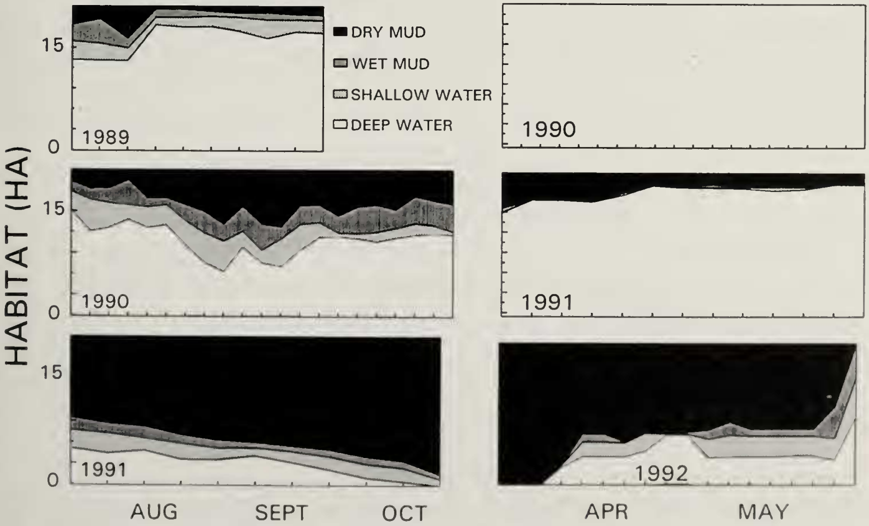


FIG. 5. Total amount of wet mud/shallow water habitat in 10 wetlands throughout the six migration seasons of the study.

TABLE 2
SHOREBIRD RESPONSES TO FIRST APPEARANCE OF WET MUD/SHALLOW WATER HABITAT WITHIN AND BETWEEN SEASONS IN SEVERAL WETLANDS

	Presence of shorebird species in wetland[a]								
	SESA	WESA	LESA	WRSA	BASA	GRYE	LEYE	STSA	LBDO
Within season[b]									
Fall 90 (N = 4)	−	+	−		+	−	+	+	+
Spring 91 (N = 5)	−		+	+	+	−	+	+	+
Spring 92 (N = 9)	−		−	+	+	+	+	−	+
Between seasons[b]									
Spring: no habitat available during two preceding springs (N = 4)	++		−	++	+	+	++	++	++
Spring: no habitat available during one preceding spring (N = 3)	++		+	++		+	++	++	++
Fall: no habitat available during one preceding fall (N = 9)	++	++	++		++	++	++	++	++

[a] Species codes as in Table 1. Within season: species present (+) or absent (−) at first appearance of wet mud/shallow water habitat. Between seasons: species present in ≥50% of wetlands (++); species present in 1–50% of wetlands (+); species in region but not present (−); blank cell indicates species not in region at time of survey.

[b] Wet mud/shallow water habitat first occurred in N wetlands during migration season.

Bird distribution relative to habitat.—We examined the relationship between numbers of birds and the amount of wet mud/shallow water habitat in wetlands on days selected according to total numbers of birds on the refuge and time in the season (see Methods). During spring, 71% of the selected wetland-days had no suitable habitat and no birds, 8% of

TABLE 3
RELATION BETWEEN NUMBERS OF SHOREBIRDS AND AREA OF WET MUD–SHALLOW WATER HABITAT DURING EIGHT FALL SURVEYS

Date	Number of wetlands	All shorebirds		Shorebirds associated with wet mud/shallow water	
		r	*P*[a]	*r*	*P*
14 Aug. 89	12	0.639	0.0125	0.615	0.017
31 Aug. 89	6	0.991	<0.0001	0.996	<0.0001
7 Sept. 89	7	0.982	<0.0001	0.977	<0.0001
10 Aug. 90	10	0.584	0.038	0.599	0.034
22 Aug. 90	11	0.723	0.006	0.720	0.006
4 Sept. 90	11	0.761	0.003	0.764	0.003
14 Sept. 90	11	0.300	0.370	0.360	0.138
26 Sept. 90	10	0.915	<0.0001	0.928	<0.0001

[a] *P* values are one-tailed.

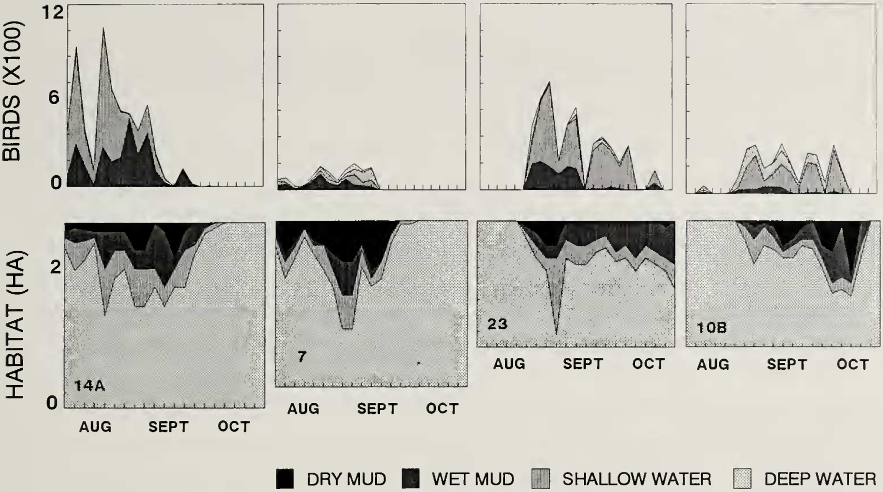


FIG. 6. Shorebird numbers associated with four microhabitats in four wetlands during the fall 1990 migration season.

the wetland-days had some available habitat but no birds, and 21% of the wetland-days had available habitat and some birds present (Fig. 6). In the late summer-fall seasons of 1989 and 1990, we found significant positive correlations between number of shorebirds and amount of wet mud/shallow water habitat on seven of eight selected days (Table 3). We were not able to quantify this trend during spring because there were not enough water units with wet mud/shallow water habitat to do so.

During six seasons of capturing and banding birds as part of a related study, we found limited evidence of individual birds returning to sites near where they had been originally banded. Of 2048 shorebirds captured between 1 Aug 1989 and 5 June 1992, five were recaptures of birds originally banded at Cheyenne Bottoms Wildlife Area (WA), Kansas, ca 30 km north of Quivira NWR. Four of these five were recaptured at Quivira NWR in subsequent seasons when shorebird habitat was unavailable at Cheyenne Bottoms WA (pers. obs., Table 4). In addition, one Semipalmated Sandpiper banded at Quivira NWR in the spring of 1990 was recaptured one year later (Table 4).

DISCUSSION

In the Great Plains, dramatic fluctuations in water levels are commonplace, transforming large deep lakes into mudflats or agricultural fields into expanses of sheet water. In the plains, wet mud/shallow water habitats are widely dispersed and highly unpredictable in space and time (Hands

TABLE 4
BANDING HISTORY OF SHOREBIRDS RECAPTURED AT QUIVIRA NATIONAL WILDLIFE REFUGE, KANSAS

	First capture		Recapture	
Species	Date	Location	Date	Habitat at Cheyenne Bottoms
Semipalmated Sandpiper[a]	28 May 90	Quivira NWR	11 May 91	—
Semipalmated Sandpiper[b]	19 Apr. 84	Cheyenne Bottoms	21 Apr. 90	Wet mud/ shallow water
Semipalmated Sandpiper[b]	30 Apr. 87	Cheyenne Bottoms	25 Apr. 92	Dry mud
Least Sandpiper[c]	25 Aug. 89	Cheyenne Bottoms	03 Aug. 90	Deep water
Semipalmated Sandpiper[c]	4 Aug. 90	Cheyenne Bottoms	08 Aug. 90	Deep water
Semipalmated Sandpiper[c]	25 Aug. 90	Cheyenne Bottoms	18 Sept. 91	Deep water

[a] Banded during this study.
[b] Banded by E. F. Martinez.
[c] Banded by G. Castro.

et al. 1991, Skagen and Knopf 1993). Even one of the largest and most stable wetlands in the central plains, Cheyenne Bottoms WA in central Kansas, suffers periodic drought and has no shorebird habitat during some migration times (Castro et al. 1990). The amount of wet mud/shallow water habitat is a complex function of many factors, including water level, topography of the wetland basin, wind action, and responses of vegetation and invertebrates to wetland conditions. Furthermore, water levels result from the combined effects of factors both extrinsic and intrinsic to a wetland, such as intentional water manipulation, local rainfall, surface runoff, stream flow, groundwater seepage (Kushlan 1989), elevation relative to water table, and type of underlying soil.

Our study indicates that shorebirds are capable of locating available habitat opportunistically. Island biogeographic theory proposes that during colonization of islands by dispersing species, these species will have a better chance at striking larger "targets" or finding larger habitats than small ones (MacArthur and Wilson 1967). Because the sizes of habitat islands (wetland patches) undergo rapid fluctuations, the strong correlation between numbers of birds and the size of suitable habitat patches is consistent with rapid colonization expected through opportunistic habitat use. On the other hand, if birds exhibited strong site faithfulness and water levels fluctuated markedly, there would be little relation between amount of wet mud/shallow water habitat and numbers of shorebirds.

We also present evidence that shorebirds are capable of refueling in a specific wetland complex in consecutive years. In this study, however, we were not able to distinguish if the return of individuals occurred because habitat was available (opportunistic use) or if they intentionally returned to the same complex (site fidelity). If our birds exhibited site fidelity, the fidelity was to the larger wetland complex rather than to a particular wetland.

The interplay of habitat predictability and behavioral flexibility results in three general patterns of seasonal use of habitats, opportunistic use or colonization, traditional use, and site fidelity. Birds that exploit unpredictable resources in temporally dynamic wetlands probably rely on flexible behaviors such as opportunistic use or colonization behavior rather than fidelity to specific wetland sites (Colwell and Oring 1988). In fact, strong site fidelity to habitats that are unpredictable clearly would be maladaptive. Birds may exhibit greater site fidelity to habitats that are fairly predictable by nature, such as breeding habitats (Oring and Lank 1984, Gratto et al. 1985) or to habitats that are dynamic in a regular periodicity, such as intertidal areas (Smith and Houghton 1984). We propose that behavioral flexibility in shorebirds allows them to fine-tune resource exploitation over a broad range of habitat conditions, from the highly dynamic Great Plains wetlands to the relatively predictable coastal areas.

Clearly, a first step in conserving stopover habitats is the identification and preservation of the most predictable sites, as is underway within the Western Hemisphere Shorebird Reserve Network. In addition to specific site efforts, on the interior plains we see an urgent need for a coordinated regional approach that targets the maintenance of complexes of potential habitat to assure resource alternatives for migrating birds as local conditions vacillate (see also Reid et al. 1983). Conservation of interior-migrating shorebirds demands the availability of nearby alternative sites when traditional sites are lost (Castro et al. 1990, Smith et al. 1991). Wetland management practices that standardize water depths and fluctuations across wetland complexes generally preclude the very short-term wetland dynamics with which shorebirds evolved.

In this study, shorebirds responded to habitats at a fairly small geographic scale. At small spatial scales, however, wet mud/shallow water habitat may not always be present, and only at larger geographic scales may the effects of dramatic water fluctuations be modulated. Wide-ranging species such as migrating shorebirds are undoubtedly influenced by the regional juxtaposition of wetland complexes across the entire Great Plains.

We can compare dynamic wetlands to "shifting mosaics" of habitat patches (Bormann and Likens 1979, Baker 1989) as seen in forested ecosystems. Just as minimum sizes of nature reserves are hypothetically defined in terms of minimum land areas that exhibit stable patch mosaics (Baker 1989), the appropriate scale for managing continental stopover sites for shorebirds might be the number of wetlands that assures a high probability of suitable shorebird habitat regardless of weather regimes during migration.

ACKNOWLEDGMENTS

We thank K. L. Stone, J. R. Rupert, S. Flatland, W. H. Howe, and P. G. Kramus for field assistance, and D. Hilley and refuge personnel for logistical support and housing at Quivira National Wildlife Refuge. We thank R. W. Butler, K. J. Gutzwiller, H. Hands, D. Helmers, and L. Oring for reviews of the manuscript. This research benefitted from the interest and supplemental resources provided by J. King and C. Lively of the North American Waterfowl Management Plan's Prairie Pothole Joint Venture.

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